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Abstract: Movement and dispersal are critical processes for almost all organisms in natural populations. Understanding their causes and consequences is therefore of high interest. While both theoretical and empirical work suggest that dispersal, more exactly emigration, is plastic and may be a function of local population density, the functional relationship between the underlying movement strategies and population density has received less attention. We here present evidence for the shape of this reaction norm and are able to differentiate between three possible cues: the relative number of individuals, the presence of metabolites (chemical cues) and resource availability. We performed microcosm experiments with the ciliate model organism Tetrahymena in order to understand the plasticity of movement strategies with respect to local density while controlling for possible confounding effects mediated by the availability of different cues. In addition, we investigated how an Allee effect can influence movement and dispersal plasticity. Our findings suggest that movement strategies in Tetrahymena are plastic and density-dependent. The observed movement reaction norm was U-shaped. This may be due to an Allee effect which led to negative density dependence at low population densities and generally positive density dependence at high population densities due to local competition. This possibly adaptive density-dependent movement strategy was likely mediated by chemical cues. Our experimental work in highly controlled conditions indicates that both environmental cues as well as inherent population dynamics must be considered to understand movement and dispersal.

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Density-dependent movement and the consequences of the Allee effect in the model organism *Tetrahymena*

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Summary

1. Movement and dispersal are critical processes for almost all organisms in natural populations. Understanding their causes and consequences is therefore of high interest. While both theoretical and empirical work suggests that dispersal, more exactly emigration, is plastic and may be a function of local population density, the functional relationship between the underlying movement strategies and population density has received less attention.

2. We here present evidence for the shape of this reaction norm and are able to differentiate between three possible cues: the relative number of individuals, the presence of metabolites (chemical cues) and resource availability.

3. We performed microcosm experiments with the ciliate model organism *Tetrahymena* in order to understand the plasticity of movement strategies with respect to local density while controlling for possible confounding effects mediated by the availability of different cues. In addition, we investigated how an Allee effect can influence movement and dispersal plasticity.

4. Our findings suggest that movement strategies in *Tetrahymena* are plastic and density-dependent. The observed movement reaction norm was u-shaped. This may be due to an Allee effect which led to negative density-dependence at low population densities and generally positive density-dependence at high population densities due to local competition. This possibly adaptive density-dependent movement strategy was likely mediated by chemical cues.

5. Our experimental work in highly controlled conditions indicates that both

environmental cues as well as inherent population dynamics must be considered to understand movement and dispersal.

Keywords

density-dependent dispersal, density-dependent movement, movement, emigration, *Tetrahymena*, microcosm, Allee effect, chemical cue, metapopulation

Introduction

Dispersal is a central process for natural populations, as it links local populations to each other such that they form spatially structured populations (e.g. metapopulations; Hanski & Gaggiotti, 2004; Fronhofer *et al.*, 2012). Such a spatial structure may affect local population dynamics by preventing stochastic extinctions via rescue effects (Brown & Kodric-Brown, 1977). Dispersal also is a key factor for community assembly and thus influences diversity patterns (Chave, Muller-Landau & Levin, 2002; Nathan, 2006). Finally, on a more macroscopic scale, dispersal, together with local adaptation, determines the geographical distribution of species (for a recent review on dispersal ecology and evolution and range dynamics see Kubisch *et al.*, 2014). Therefore, understanding the causes and consequences of dispersal is an important aim in ecological and evolutionary research (Clobert *et al.*, 2012).

Dispersal comprises three more or less distinct phases: emigration, transition and immigration (Clobert *et al.*, 2012). During all three phases, the acquisition, processing and use of external, internal and social information plays an important role for the subsequent movement and dispersal decisions (Bowler & Benton, 2005; Clobert *et al.*, 2009). Natural selection will favour such condition-dependent movement and dispersal rules over uninformed strategies, as it gives individuals fitness advantages except if either the acquisition of information or the subsequent behavioural changes are too costly (Bowler & Benton, 2005; Nathan *et al.*, 2008; Clobert *et al.*, 2009; Hovestadt, Kubisch & Poethke, 2010). Possible sources of information are, for example, local conspecific density (Matthysen, 2005; De Meester & Bonte, 2010; Fellous *et al.*, 2012; Kuefler, Avgar & Fryxell, 2013; Bitume *et al.*,

2013; Pennekamp *et al.*, 2014), relatedness (Bitume *et al.*, 2013), patch size (Crone, Doak & Pokki, 2001; Altermatt & Ebert, 2008, 2010), the presence of other species (Hauzy *et al.*, 2007) or food availability (Kuefler, Avgar & Fryxell, 2012, 2013).

Here we focus on the effects of intra-specific density on movement strategies (density-dependent movement, DDM), because movement is the microscopic process from which dispersal emerges (see e.g. Nathan *et al.*, 2008; Revilla & Wiegand, 2008). Of course, movement behaviour is not exclusively a proxy for dispersal. For example, movement is also linked to foraging or mate-finding, reflecting spatial displacement without implying spatial gene flow. For the sake of simplicity we will here focus on movement seen as the basis of dispersal. We understand density as the number of individuals relative to the carrying capacity, and not relative to patch area or volume as the latter are not species-specific characteristics.

Functional relationships capturing the effect of density on dispersal have been formally derived from first principles only for density-dependent emigration (DDE) by Metz & Gyllenberg (2001) for continuous-time systems and by Poethke & Hovestadt (2002) for discrete-time metapopulations (for ecological and evolutionary impacts of DDE see e.g. Amarasekare, 2004; Hovestadt & Poethke, 2006; Enfjäll & Leimar, 2009; Travis *et al.*, 2009; Kubisch, Poethke & Hovestadt, 2011; Altwegg *et al.*, 2013). The logic that emigration is selected for as long as the expected inclusive fitness of an emigrant is higher than the expected inclusive fitness of a resident individual leads to a threshold model: individuals should not emigrate as long as local population densities are low enough. Beyond this threshold the functional relationship depends somewhat on the model assumptions, leading to a step function in continuous-time models (Metz & Gyllenberg, 2001) or to a simple asymptotic function above the threshold for discrete-time models (Poethke & Hov-

estadt, 2002). Similar ideas can be found in Ruxton & Rohani (1998) who have developed a model of fitness-dependent dispersal in metapopulations. In summary, emigration rate and population density (as a proxy for competition for any kind of resources) are fundamentally positively related. This relationship may be different for (very) small population sizes in species that suffer from an Allee effect. Allee effects are generally defined as a positive correlation between population density and individual fitness (Allee, 1931; Courchamp, Berec & Gascoigne, 2008). This leads to reduced fitness at small population densities which may be due to the lack of social interactions or reduced mating opportunities, for example. In such a scenario DDE may have a negative slope at low densities but will become positive again at higher densities leading to a roughly u-shaped function (see Figure 1).

While these theoretical predictions are straightforward, empirical evidence is somewhat confusing and ambiguous. Positive density-dependence has been found across many taxa (protists: Hauzy *et al.* 2007; rotifers: Kuefler, Avgar & Fryxell 2012; mites: Bitume *et al.* 2013; aquatic insects: Fonseca & Hart 1996; collembolans: Bengtsson, Hedlund & Rundgren 1994; spiders: De Meester & Bonte 2010; butterflies: Nowicki & Vrabec 2011; birds and mammals, for a review see: Matthysen 2005). However, also an overall negative density-dependence has been reported across a similar diversity of organisms (protists: Fellous *et al.* 2012 and depending on genotypes Pennekamp *et al.* 2014; damselflies: Rouquette & Thompson 2007; butterflies: Baguette, Clobert & Schtickzelle 2011; black bears: Roy *et al.* 2012; birds and mammals, for a review see: Matthysen 2005). A noteworthy study has been conducted by Kim, Torres & Drummond (2009) who report a u-shaped density-dependent dispersal function, such as we describe above, in a colonial marine bird, the Blue-footed Booby. In addition to providing conflicting evidence

about density-dependent dispersal, which may be due to different ranges of densities considered, most of these efforts concentrate uniquely on emigration strategies and do not analyse the underlying movement patterns (but see Kuefler, Avgar & Fryxell, 2012, 2013).

We here aimed at filling this gap by testing whether and how movement strategies (reaction norms; see Clobert *et al.* 2009) are plastic with respect to population density in organisms with an Allee effect. For our study we used the model organism *Tetrahymena*, which is known to have an Allee effect (e.g., Christensen *et al.*, 2001; Chaine *et al.*, 2010). We used microcosm experiments (Jessup *et al.*, 2004; Benton *et al.*, 2007) because this approach allows us to carefully pinpoint the relevant cues, such as the 1) relative number of individuals, 2) chemical cues or 3) resource availability, used for DDM. In these tightly controlled experimental settings we can individually manipulate these parameters and achieve a suitable level of replication.

We addressed three questions: 1) Are movement strategies (characterized by velocity and the turning angle distribution) density-dependent and shaped by adaptation to an Allee effect? 2) What proximate cues (i.e., relative number of individuals, chemical cues or resource availability) are used for density-dependent movement? 3) How do these microscopic processes translate to the regional scale by affecting population spread (net distance travelled, diffusion coefficient)?

We generally predict a u-shaped DDM function as an evolutionary consequence of the Allee effect (see also figure 1) as movement and dispersal were shown to correlate in *Tetrahymena* (Pennekamp, 2014). Our detailed predictions regarding the influence of the three potential density cues (i.e., relative number of individuals, chemical cues or resource availability) on movement strategies are illustrated in

figure 2. We always include a prediction for the case that a specific density cue is used in an adaptive way to mediate DDM as well as an alternative prediction for the case that this cue has concominant effects that cannot be interpreted as adaptive DDM.

Materials and methods

Study organism

We used the freshwater protist *Tetrahymena* cf. *pyriformis* (Foissner pers. comm.; Simon, Nanney & Doerder 2008) as a model organism. This small ciliate (approx. 35 ± 5 μm along the major body axis under our laboratory conditions) exhibits high growth rates and carrying capacities (approx. $2 < r_0 < 4$ per day and $6000 < K < 10000$ per ml; see also figure 6 A) which makes it an ideal study organism for answering ecological and evolutionary questions (e.g. Fjerdingstad *et al.*, 2007; Hauzy *et al.*, 2007; Schtickzelle *et al.*, 2009; Altermatt, Schreiber & Holyoak, 2011; Carrara *et al.*, 2012; Giometto *et al.*, 2014). Importantly, *Tetrahymena* species are known to suffer from an Allee effect (e.g., Christensen *et al.*, 2001). The resulting conspecific attraction made them a model organism for the study of cooperative behaviour (e.g. Schtickzelle *et al.*, 2009; Chaine *et al.*, 2010).

We kept *Tetrahymena* in protist medium (Protozoan pellets; Carolina Biological Supply; 0.46 gl^{-1}) at a constant temperature of 22°C (for a detailed description see Altermatt, Schreiber & Holyoak, 2011; Carrara *et al.*, 2012). Resources were supplied as 5% dense bacterial culture (approx. one week old; *Serratia fonticola*, *Bacillus subtilis* and *Brevibacillus brevis*) per liter of protist medium.

Microcosm experiments

As described above, density-depend movement (DDM) can be mediated by three cues: 1) the relative number of individuals, 2) chemical cues and 3) resource availability. All three cues were manipulated separately while keeping the other two constant. All experiments were carried out in 1.5 ml tubes (Eppendorf) using a total of 1 ml protist medium and replicated five times (due to experimental failure one replicate had to be discarded from the experiment analysing the influence of the relative number of individuals). Measurements were taken 1h after the application of the treatments.

A gradient in cell densities was generated by diluting centrifuged cultures (see Fjerdingstad *et al.*, 2007) of five days old populations of *Tetrahymena*. These cultures were assumed to be at carrying capacity (see figure 6 A for a growth curve). Dilution yielded five levels of population densities ("relative number of individuals"): 0.1, 0.5, 0.75, 1 and 1.5 times the carrying capacity. The carrying capacity (K) was estimated to be about 8600 individuals (see figure 6 A). To keep resources and metabolites constant we added 5% bacterial culture to all treatments and the dilution was carried out with filtered protist medium from the original cultures (filter pore size 0.2 μm).

Resource content was manipulated by adding diluted bacterial cultures. This resulted in the following six levels of relative resource concentration ("fraction bacterial culture"): 0, 0.005, 0.025, 0.05, 0.25 and 0.5. *Tetrahymena* metabolites (chemical cues) were kept constant by diluting the bacteria with fresh medium and by always using the same amount of *Tetrahymena* culture. The relative number of individuals was fixed to about half of the carrying capacity.

Chemical cues were manipulated in analogy to the other two factors, namely by adding dilutions of filtered medium (filter pore size $0.2\mu m$) from a three weeks old *Tetrahymena* culture. We chose the following concentration levels ("fraction old medium"): 0, 0.005, 0.025, 0.05, 0.25 and 0.5. We used old medium instead of directly adding possible chemical cues to fresh medium (as was done e.g. by Kovacs, Lovas & Csaba, 1994) in order to guarantee that we were operating in a biologically plausible range of concentrations. This approach has been previously used by Fellous *et al.* (2012), for example. Evidently, we thereby loose some degree of control over the system and are not able to distinguish directly between the effects of different chemical compounds.

To quantify the combined effect of all three possible cues on movement strategies as well as to obtain equilibrium densities and growth rates for our study species we followed population growth over four days in six replicated populations grown in 20 ml vials (Sarstedt) with 15 ml medium. On day zero, these populations were inoculated with 1ml of *Tetrahymena* taken from a batch culture. We fitted a logistic growth function of the form $N(t) = \frac{K}{1+e^{a-r_0 t}}$ with $a = ln(\frac{K}{N(0)} - 1)$ where K is the carrying capacity and r_0 is the growth rate using a non-linear least squares approach (statistical software R; version 3.0.2; function "nls").

Data collection

After one hour of treatment, the populations in the microcosms were sampled and we used video analysis to collect data on movement behaviour (velocities, turning angle distribution, net distance travelled, diffusion coefficient; see also Giometto *et al.* 2014). We followed the protocol proposed by Pennekamp & Schtickzelle

(2013) using the free image analysis software ImageJ (version 1.46a) with the MOSAIC particle tracker plugin (Sbalzarini & Koumoutsakos, 2005).

Videos were recorded for 20 s (total of 500 frames) at a 30-fold magnification (imaged sample volume: 19 μl; height: 0.5 mm) using a Nikon SMZ1500 stereomicroscope with a Hamamatsu Orca Flash 4 video camera. The image analysis first determines the location of moving particles of a predefined size range (determined through preliminary trials to be an area between 20 and 200 pixels) for every frame of the video by subtracting the information for two subsequent frames ("difference image"). In a second step these locations are re-linked in order to obtain individual movement paths. For the linking procedure we used the MOSAIC particle tracker plugin. The algorithm is described in detail in Sbalzarini & Koumoutsakos (2005). In brief, the algorithm links particles identified in subsequent frames using a link distance (here set to 15 pixels). Linking can occur over more than two subsequent frames (here the relevant parameter is set to 3). The tracker plugin allows for particles to disappear and if it is unable to infer a link the trajectory is terminated. For further details please also refer to the protocol described in detail by Pennekamp & Schtickzelle (2013).

Statistical analysis

The recorded movement paths allowed us to calculate descriptive indices of the movement behaviour such as velocity and circular standard deviation of the turning angle distribution as well as the net distance travelled, that is the Euclidean distance travelled. In order to obtain best estimates, we only included movement paths of individuals that could be observed during a minimum of a fifth of the total

video time (4s). We used the statistical software R (version 3.0.2; packages "adehabitatLT" version 0.3.14 and "circular" version 0.4-7; see also Pewsey, Neuhäuser & Ruxton 2013) to perform all analyses. In addition, we calculated the diffusion coefficient (i.e., the linear slope of mean square displacement over time) as a measure of population spread. The data can be downloaded from Dryad (Fronhofer, Kropf & Altermatt, 2014).

As Turchin (1998) noted, the turning angle distribution might suffer from autocorrelation due to oversampling of the movement path. In order to exclude any artifacts arising from our sampling method we ran additional analyses with simplified movement paths. We only kept coordinates of the movement paths which were farther than a certain threshold (1, 2, 3, ..., 25 pixels) from the straight line connecting the two locations surrounding it (for a detailed description see Pennekamp, 2014). This was done using the Douglas-Peucker algorithm (statistical software R version 3.0.2; package "rgeos" version 0.3-3, function "gSimplify"). We selected the minimal threshold for every movement path individually by iteratively increasing the threshold until no significant autocorrelation could be detected (package "adehabitatLT" version 0.3.14 function "testang.ltraj"). The results of these analyses are reported in the supporting information figure S1. Although the relationship between the width of the turning angle distribution and density was impacted by oversampling it was not altered fundamentally. We chose to report the original, unmodified data in the main text as removing the autocorrelation also implies losing information about the biologically relevant autocorrelation.

We analysed the individual level movement data (velocity, standard deviation of the turning angle distribution, net distance travelled) with linear mixed models or with generalized linear mixed models (in case assumptions of linear models

were violated) using the statistical software R (version 3.0.2; functions "lmer" and "glmer" from the "lme4" package version 1.0-4). In order to account for possible non-independence of individuals within one replicate we used "replicate" as a random effect. The analysis of the diffusion coefficient was carried out analogously with the difference that there was only one data point per replicate since the diffusion coefficient is a population level metric. We therefore did not include "replicate" as a random effect and used linear models. After visual inspection, we either fitted linear, squared or cubed polynomials to the data and used AIC for model selection (optimizing the maximum likelihood criterion as we compare models with different fixed effects). We always added the null model for comparison and selected the best fitting model. This allowed us to infer the shape of population level reaction norms.

Results

Relative number of individuals

Velocity was found to be independent of the relative number of individuals present (AIC(linear) = -10420.44, AIC(null) = -10421.83; figure 3 A). By contrast, the width of the turning angle distribution quantified as its standard deviation increased significantly with more individuals (AIC(linear) = -5392.87, AIC(null) = -5345.12; figure 3 B). These changes in the turning angle distribution led to an overall negative slope for the net distance travelled (AIC(linear) = 5113.41, AIC(null) = 5180.43; figure 3 C; see supporting information figure S2 A for the diffusion coefficient and figure S3 for a plot with the measured densities on the x-axis).

Chemical cues

The relationship between movement strategies and chemical cues was clearly more complex (see figure 4): velocity was found to be a non-monotonic function of the concentration of chemical cues. While very small concentrations led to faster movements, the same was true for high concentrations (figure 4 A). Yet, swimming speed decreased again for very high amounts of chemicals (AIC(cubic) = -4934.75, AIC(quadratic) = -4915.59, AIC(linear) = -4893.6, AIC(null) = -4829.19). We observed the exact opposite pattern for the width of the turning angle distribution: straighter movements for low and high concentrations of chemical cues with a subsequent increase in turns for the highest value (AIC(cubic) = -2465.43, AIC(quadratic) = -2428.41, AIC(linear) = -2380.28, AIC(null) = -2358.05; figure 4 B). Taken together these changes in velocity and movement straightness led to larger displacements at low and high concentrations of chemical cues and a drop in the distance covered for the highest concentration (AIC(cubic) = 2556.14, AIC(quadratic) = 2562.52, AIC(linear) = 2568.16, AIC(null) = 2570.16; figure 4 C; see supporting information figure S2 B for the diffusion coefficient).

Resource availability

Finally, we analysed the effect of resource availability on movement strategies (figure 5). We observed a significant increase in velocity at higher resource concentrations before a saturation was reached (AIC(quadratic) = -6775.7, AIC(linear) = -6757.76, AIC(null) = -6658.9; figure 5 A). A similarly positive relationship could be found for the width of the turning angle distribution (AIC(linear) = -3406.66, AIC(null) = -3394.54; figure 5 B). This combination of slow but relatively straight

movement for low resource concentrations and faster but less straight movement at high concentrations made the overall observed displacement not significantly related to resource availability (AIC(linear) = 2897.34, AIC(null) = 2897.05; figure 5 C; see supporting information figure S2 C for the diffusion coefficient).

Population growth and the combined effect of all three cues

In order to explore the effect of all three cues combined in their biologically relevant relative densities and concentrations we additionally recorded movement patterns in non-manipulated, growing populations (figure 6). The growth curve (figure 6 A) allowed us to estimated the carrying capacity to approximately $K = 8600$ individuals per ml and the growth rate $r_0 = 4$ per day. Over time — which here implied increasing population density, decreasing resource availability as well as an increasing concentration of chemical cues — both velocity (figure 6 B; AIC(cubic) = -23307.07, AIC(quadratic) = -23194.38, AIC(linear) = -22875.88, AIC(null) = -21024.78) and the width of the turning angle distribution (figure 6 C; AIC(cubic) = -11113.95, AIC(quadratic) = -10977.870, AIC(linear) = -10488.71, AIC(null) = -9707.48) were downwards u-shaped. Together, these effects resulted in an upwards u-shaped relationship between net distance travelled and time, respectively population density (figure 6 D; AIC(cubic) = 12119.25, AIC(quadratic) = 12120.21, AIC(linear) = 12146.75, AIC(null) = 12202.83; see supporting information figure S4 for the diffusion coefficient).

Discussion

Our experiments show that movement in *Tetrahymena* was plastic with regard to density. More specifically, we found evidence for a u-shaped relationship (figure 6) between movement and density. We speculate that this reaction norm is the signature of the evolutionary consequence of an Allee effect and of local competition. Furthermore, we tentatively suggest that in *Tetrahymena*, DDM is mediated by chemical cues (figures 3, 5 and 4).

Relative number of individuals and resource availability

The response elicited by the relative number of individuals (figure 3) corresponds to the prediction depicted in figure 2 B. Although *Tetrahymena* did not show slower movements with increasing density, the width of the turning angle distribution increased significantly. Following our prediction we interpret this as a physical effect of crowding: when more individuals are present, encounter rates increase and straight-line movements are less likely (figure 3 B). Less straight-line movements were directly reflected in reduced displacement (figures 3 C and S2 A). We suggest that the relative number of individuals is not used as a cue for DDM because negative DDM (or DDE) due to an Allee effect should be restricted to low densities as Allee effects only affect low density populations. If resources are limited, competition will most likely lead to positive DDM and DDE at higher densities (Metz & Gyllenberg, 2001; Poethke & Hovestadt, 2002). Of course, the slope will depend on the cost-benefit calculation that takes into account the strength of local competition, movement and dispersal costs (Bonte *et al.*, 2012) and the expected inclusive fitness of the emigrant.

The plastic response we observed in relation to the amount of resources available (figure 5) is best explained by metabolic effects of increased energy availability, probably also by foraging behaviour and not by DDM. As predicted in figure 2 F velocity increased with increasing resource availability (figure 5 A). This is contrary to what we had expected if resources were used as a cue for DDM, as lower resource concentrations can be interpreted as increased competition which should trigger emigration (figure 2 E). At the same time we observed an increased occurrence of turns in the movement paths (figure 5 B). This can be interpreted in two ways, which are not mutually exclusive: 1) If turns are costly (Wilson *et al.*, 2013), more resources will allow individuals to perform more turns. 2) Alternatively, more turns can be emergent phenomenon of more or less systematic search behaviour for food in resource-rich environments (see Kareiva & Odell 1987 and Benhamou 1992 for area-restricted search strategies; Fronhofer, Hovestadt & Poethke 2013 for non-random within patch search). Displacement was not affected by the amount of resources present (figure 5 C and S2 C) as the effects of faster and less straight movements cancel each other out.

Chemical cues potentially mediate density-dependent movement

The results we obtained for chemical cues (figure 4) correspond to our predictions for DDM (figure 2 C), except for the highest concentration. We observed fast and straight movements at very low as well as at high concentrations of chemical cues (figure 4 A and B). We suggest that this led to negative DDM for low and positive DDM for high concentrations respectively (figure 4 C and S2 B).

Although we did not determine the chemical composition of the "old" medium we used for these experiments, we can formulate an educated guess about possibly important compounds, which can be used as cues for population density, based on biomedical studies that use *Tetrahymena* as a model organism (e.g. Rasmussen *et al.*, 1996; Rasmussen & Rasmussen, 2000; Christensen *et al.*, 2001; Csaba, 2012). Cell death at low population densities (Allee effect) is most likely regulated through intra-cellular signalling, as low-density populations can be rescued by the addition of cGMP or protein kinase activators. The addition of low concentrations of insulin (10^{-14} to 10^{-11} M) had comparable effects which suggests that insulin-mediated signal transduction pathways are involved (for a review see e.g. Rasmussen *et al.*, 1996). Note that although most of these studies were performed with *Tetrahymena thermophila* the findings are very likely applicable not only to other *Tetrahymena* species but also to a wide range of other unicellular eukaryotes (Christensen *et al.*, 1997).

The decrease in velocity and net distance travelled we observed at the highest concentration of chemical cues (figure 4) is consistent with previous studies (Kovacs, Lovas & Csaba, 1994, these authors used concentrations of $10^{-6}M$ versus 10^{-14} to $10^{-11}M$ used to rescue cells at low densities) and is probably due to a negative effect of high concentrations of metabolites such as insulin on swimming speed (as depicted in figure 2 D).

Based on these interpretations and our predictions (illustrated in figure 2) we hypothesize that such chemical compounds (or the lack thereof) can reliably indicate local population density, which is not the case for resource availability, for example. Chemical cues may also be less costly for estimating the presence and abundance of conspecifics, rather than perceiving the relative number of actively

moving organisms directly. Note that these conclusions strongly depend on the cubic fit we observe in figure 4 which is determined by the values observed for one concentration (0.25). In addition, the general value of chemical cues for eliciting density-dependent behaviour remains to be established as Fellous *et al.* (2012), for example, found no effect of such metabolites on emigration behaviour in the freshwater protozoan *Paramecium caudatum*.

While the lack of a statistical relationship in the latter study may not necessarily reflect the absence of an effect in general, it nevertheless shows that the detection might depend on the specific experimental set-up. Our results are consistent with previous work by Hauzy *et al.* (2007) on predator-induced dispersal who found that chemicals emitted by predatory protists were used as a cue for emigration in *Tetrahymena*. We are confident that an analogous mechanism can be relevant to sense intra-specific density.

Allee effects and local competition likely shape the reaction norm

In the light of our predictions (figures 1 and 2) we speculate that the u-shaped DDM reaction norm reported in figure 6 results from the interaction of the Allee effect and local competition: Reduced fitness at both low and high population densities has the potential to select for movement and dispersal as a means to escape from these conditions.

Our results suggest that the width of the turning angle distribution is a major determinant of displacement in *Tetrahymena*. The downwards u-shape we observed reflects the pattern measured for chemical cues alone (figure 4 B) without the effect

of very high concentrations. This is not surprising since the culture used as a donor of chemical cues in figure 4 was more than three times as old as the cultures in figure 6. We here cannot exclude that the relative number of individuals (figure 3) plays a role as a cue for negative DDM at low densities (figure 6; note the different x-axes when comparing figures 3, 4 and 6). Yet, as the width of the turning angle distribution decreases again for densities approaching carrying capacity (figure 6 C) we suggest that chemical cues are the more relevant, at least at high population densities.

We assume that the shape of the curve for velocity (figure 6 B) is influenced by an interaction between chemical cues and high resource availability, which might have increased velocity overall (compare the y-axes of figures 4 and 6) and decreased the relative difference between the first values. Nevertheless, the net distance travelled (figure 6 D) clearly shows the predicted u-shaped relationship for DDM (and DDE, if one assumes a simple scaling) in species with an Allee effect.

Comparisons and conclusions

Our findings are in good accordance with recent work by Kuefler, Avgar & Fryxell (2012) who showed that diffusion is positively density-dependent in a rotifer species. Here, we did not consider the internal state of our study organism but were interested in a more mechanistic analysis of the external factors, such as density and relevant cues, and relating them in full detail to three aspects of the movement path: velocity, turning angle distribution and displacement. This allowed us to interpret the negative relationship reported in the experiment in which we manipulated the relative number of individuals as an effect of crowding.

Similarly, Kuefler, Avgar & Fryxell (2013) analysed the impact of resource concentration and conspecific density. They could show that the presence of resources increased the number of turns in a one-dimensional landscape, indicating that the presence of competitors affected velocity, which then led to more displacement. The reaction norms we measured confirm these findings, except for the effect of resources on velocity which is inverted here. We suggest that this is due to a positive metabolic effect linked to resource intake and that our study organisms were more resource limited.

In conclusion, our study allows us to tentatively generalize DDM (and by extension DDE) to organisms that have an Allee effect (for examples see Courchamp, Berec & Gascoigne, 2008). In this light our experiments (especially figure 6 D) are a confirmation of the hypothesis expressed by Kim, Torres & Drummond (2009) who provided first correlational evidence that dispersal propensity follows a u-shaped function in species with an Allee effect. This suggests that discussions about whether DDE or DDM exhibit globally positive or negative slopes might be misleading, as both conditions can be found in u-shaped reaction norms, depending on whether data were collected for generally low or high densities.

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422 Data accessiblity

423 The data are available at Dryad: http://doi.org/10.5061/dryad.383q4.

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Figure captions

Figure 1. Density-dependent emigration (DDE) in continuous-time (A) and discrete-time models (B) including an Allee effect. These relationships were derived by Metz & Gyllenberg (2001) for time continuous and by Poethke & Hovestadt (2002) for time discrete systems from first principles based on a marginal value approach (black lines). We added the most likely consequence of an Allee effect, that was not included in the original DDE functions (grey lines). In contrast to DDE at high densities in discrete time systems, we propose that an Allee effect should lead to a second threshold, as below this critical density threshold emigration should always be an ESS.

Figure 2. Qualitative predictions of density-dependent movement (DDM) reflecting the evolutionary consequences of an Allee effect and local competition. We predict 1) a concave up response for velocity (A, black) and a concave down response for the width of the turning angle distribution (A, grey) if the relative number of individuals (physical contacts) is used as a cue for DDM. This combination would lead to a u-shaped function for population spread (A, inset). However, a purely physical effect of crowding, leading to lower velocities and/or stronger turns as well as a decreasing net distance travelled, can also be predicted (B). 2) Chemical cues (any substance secreted by the study organism) may be used to trigger DDM and should lead to the same u-shaped response as predicted for the relative number of individuals (C). Yet, such chemical cues may also have direct negative effects on *Tetrahymena* (Kovacs, Lovas & Csaba, 1994) leading to less turns and slower movements (D). 3) Trivially, low resource availability should

trigger faster and straighter movement as an escape mechanism (E). As high resource availability is probably not a good indicator of low population densities we do not predict a u-shaped reaction norm in this case. Clearly, the predictions depicted in (E) can also be interpreted as an effect of local foraging. Finally, a purely metabolic effect of resource availability (F) might allow faster movements and stronger turns if these are costly (Wilson *et al.*, 2013). Higher velocities and more turns may cancel each other out resulting in a more or less flat relationship for displacement. In contrast to the relationships shown in figure 1 these functions are purely qualitative and not derived from first principles. Note that the location of the carrying capacity on the x-axes is of specific interest. Yet, as the exact shape of the reaction norms will depend on the cost-benefit ratio of moving, which has to take into account movement costs or the mean expected inclusive fitness of individuals moving to new patches, for instance, we cannot exactly pinpoint the location of K. It should, however, roughly be located in the centre of the axes.

Figure 3. Effect of the relative number of individuals. The three panels depict the effect of conspecific density (measured relative to the carrying capacity, K) on movement strategies of *Tetrahymena* while keeping the two other possible cues (the amount of resources and the concentration of chemical cues) constant. Velocity was found to be independent of population density (LMM(null); N = 3716(4). As sample size N we always report the total number of individuals and thereafter the number of replicates in brackets). By contrast, we found a significantly negative relationship for the width (s.d.) of the turning angle distribution (GLMM(linear); N = 3716(4), error distribution family: Gamma). These two aspects of movement taken together resulted in a negative slope for the net distance

travelled, which is the Euclidean distance between the starting and the end point of an individual movement path (GLMM(linear); N = 3716(4), error distribution family: Gamma). Note that the diffusion coefficient shows the same behaviour (supporting information figure S2 A). The grey circles indicate means and the error bars standard errors over the four replicates. The black squares and dotted lines are the model predictions. See supporting information figure S3 for an analogous plot with the measured number of individuals on the x-axis.

Figure 4. Effect of chemical cues. Chemical cues had a strongly non-linear effect on movement strategies. While we observed a negative slope for velocity at low concentrations of chemical cues, this effect was inverted at higher concentrations. At the highest concentration the slope became negative again (LMM(cubic); N = 1598(5)). A similarly non-linear correlation could be found for the width of the turning angle distribution. Yet, the slopes were exactly the opposite in comparison to velocity (LMM(cubic); N = 1598(5)). This combination of fast and straight movement at low and high densities as well as slow movement and strong turns for intermediate and very high concentrations of chemical cues led to larger displacement distances (and diffusion coefficients; supplementary information figure S2 B) for low and high concentrations (GLMM(cubic); N = 1598(5), error distribution family: Gamma). The grey circles indicate means and the error bars standard errors over the five replicates. The black squares and dotted lines are the model predictions.

Figure 5. Effect of resource availability. We here explored the effect of resource concentration on movement behaviour and found a non-linear positive correlation

for velocity (LMM(quadratic); N = 2286(5)) and a linearly positive relationship for the width of the turning angle distribution (LMM(linear); N = 2286(5)). The interaction of increasing speed and decreasing straightness of the movement paths prevented net distance travelled (as well as the diffusion coefficient; supplementary information figure S2 C) to correlate with resource availability (GLMM(linear); N = 2286(5), error distribution family: Gamma). The grey circles indicate means and the error bars standard errors over the five replicates. The black squares and dotted lines are the model predictions.

Figure 6. Combined effect of all three cues in non-manipulated, growing populations of *Tetrahymena*. The top panel (A) shows the corresponding growth curve and allows the reader to relate time to density for panels B–D. We observed downwards u-shaped relationships between time, respectively populations density, and both velocity (B; LMM(cubic); N = 7757(6)) and the width of the turning angle distribution (C; LMM(cubic); N = 7757(6)). The resulting net distance travelled showed an upwards u-shape (D; GLMM(cubic); N = 7757(6), error distribution family: Gamma). The same pattern was observed for the diffusion coefficient (supplementary information figure S4). The grey inter-connected circles indicate the six replicates of growing populations. The black squares and lines are the model predictions.

Figures

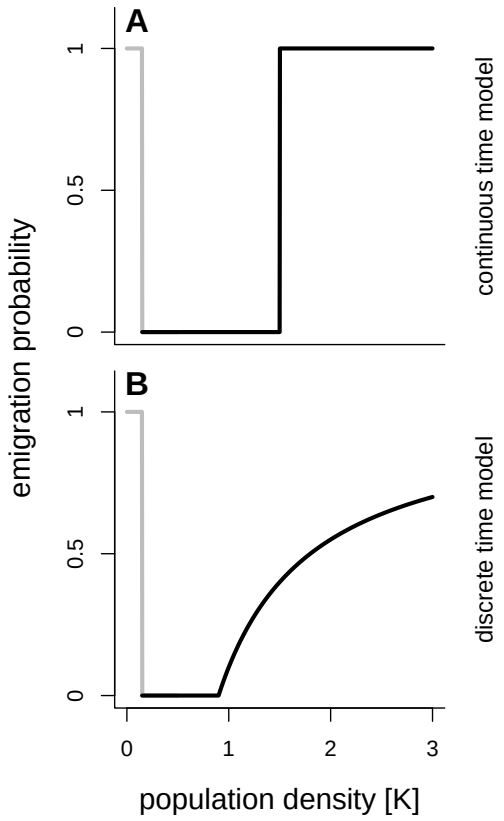

Figure 1:

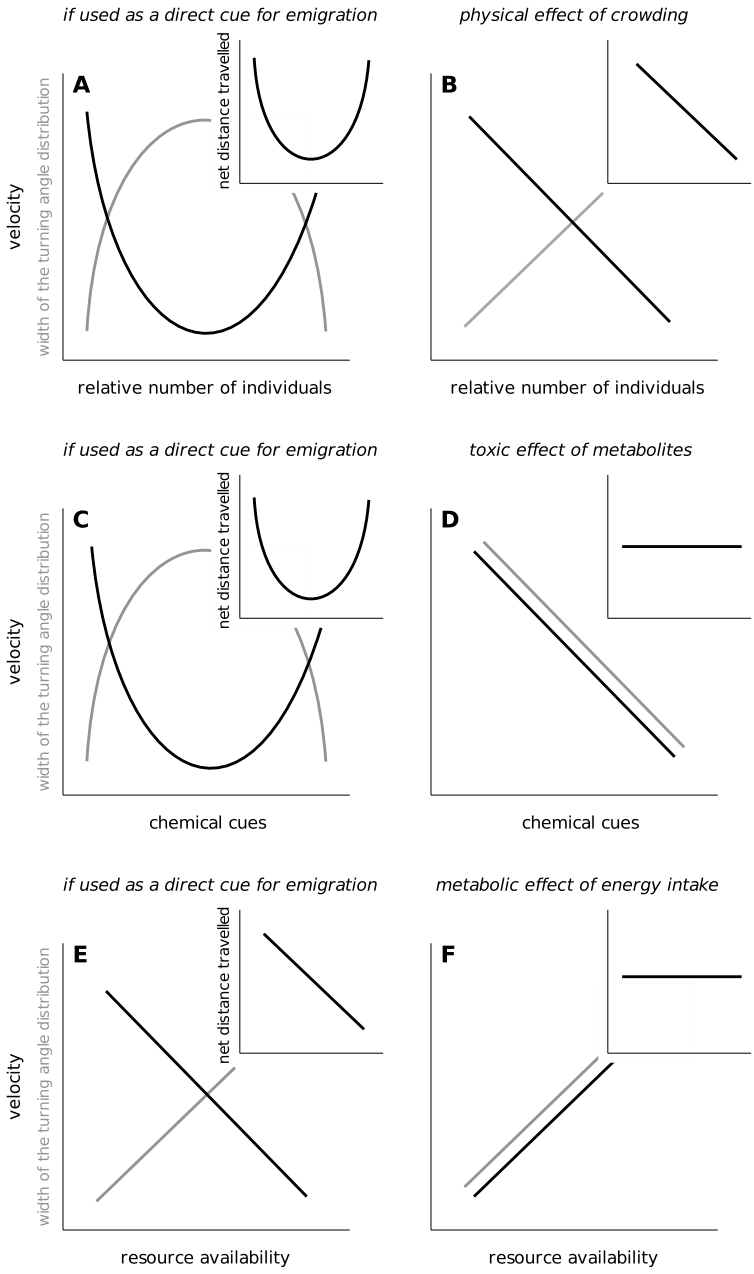
if used as a direct cue for emigration
physical effect of crowding
A
B
net distance travelled
velocity
width of the turning angle distribution
relative number of individuals
relative number of individuals
if used as a direct cue for emigration
toxic effect of metabolites
C
D
net distance travelled
velocity
width of the turning angle distribution
chemical cues
chemical cues
if used as a direct cue for emigration
metabolic effect of energy intake
E
F
net distance travelled
velocity
width of the turning angle distribution
resource availability
resource availability

Figure 2:

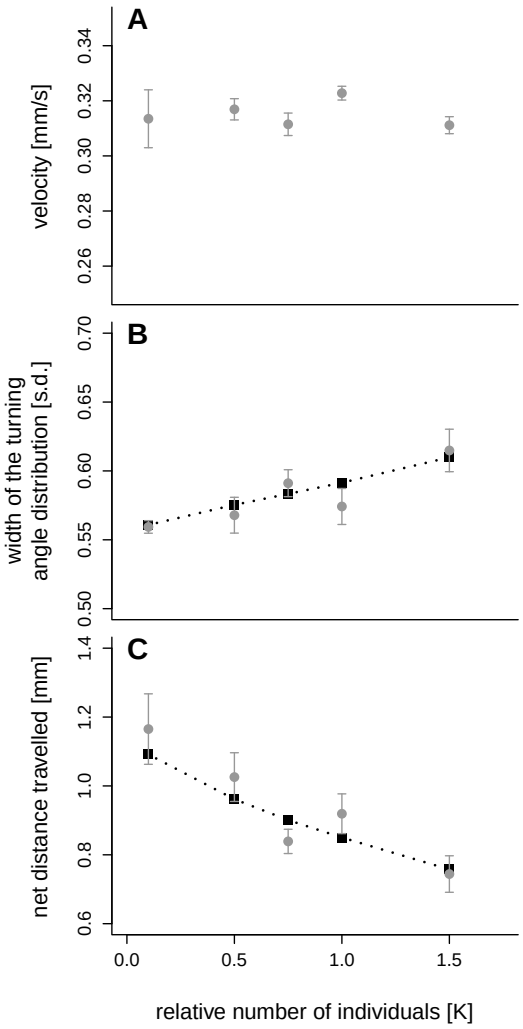
A
velocity [mm/s]
0.26
0.28
0.30
0.32
0.34
B
width of the turning
angle distribution [s.d.]
0.50
0.55
0.60
0.65
0.70
C
net distance travelled [mm]
0.6
0.8
1.0
1.2
1.4
0.0
0.5
1.0
1.5
relative number of individuals [K]

Figure 3:

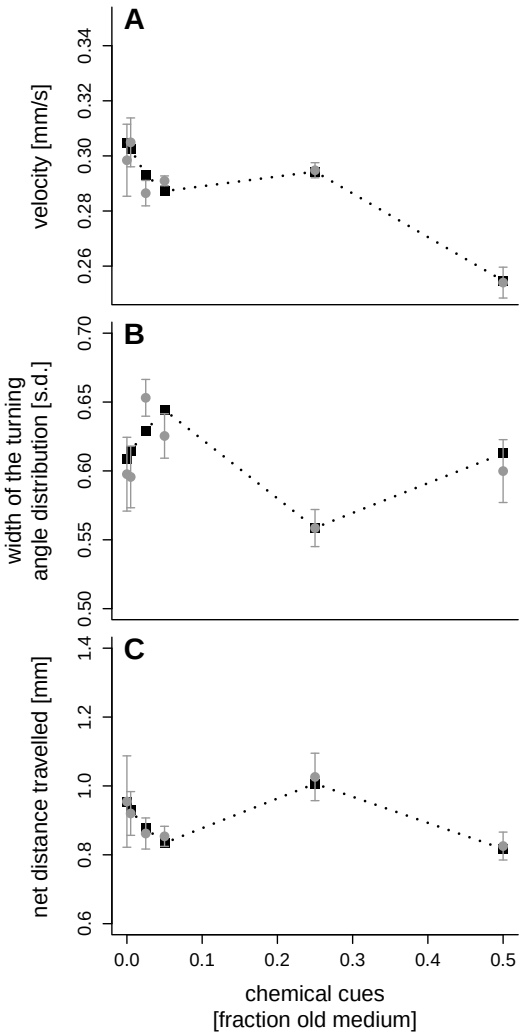
A
velocity [mm/s]
0.26
0.28
0.30
0.32
0.34
B
width of the turning
angle distribution [s.d.]
0.50
0.55
0.60
0.65
0.70
C
net distance travelled [mm]
0.6
0.8
1.0
1.2
1.4
0.0
0.1
0.2
0.3
0.4
0.5
chemical cues
[fraction old medium]

Figure 4:

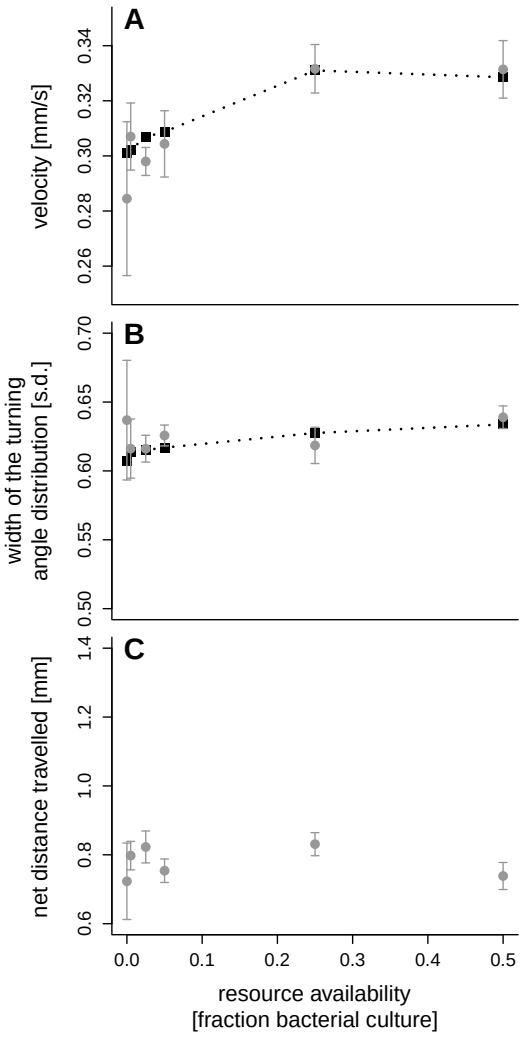
A
velocity [mm/s]
0.26
0.28
0.30
0.32
0.34
B
width of the turning
angle distribution [s.d.]
0.50
0.55
0.60
0.65
0.70
C
net distance travelled [mm]
0.6
0.8
1.0
1.2
1.4
0.0
0.1
0.2
0.3
0.4
0.5
resource availability
[fraction bacterial culture]

Figure 5:

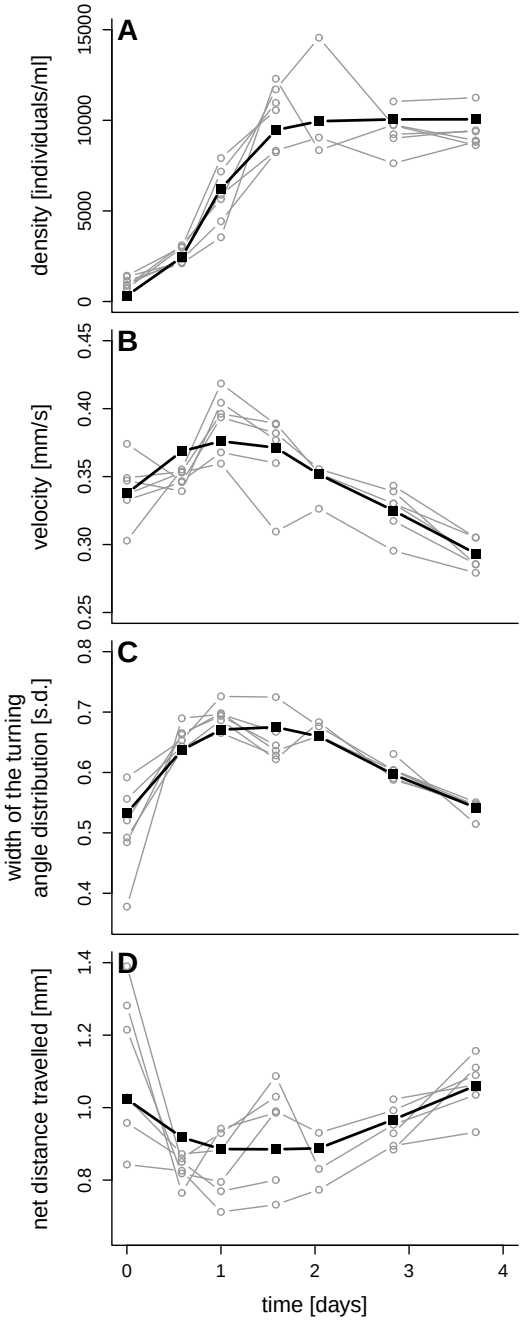
A
density [individuals/ml]
0
5000
10000
15000
B
velocity [mm/s]
0.25
0.30
0.35
0.40
0.45
C
width of the turning
angle distribution [s.d.]
0.4
0.5
0.6
0.7
0.8
D
net distance travelled [mm]
0.8
1.0
1.2
1.4
0
1
2
3
4
time [days]

Figure 6: